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To cite this article: Dr Helen B. Anderson, Dr James D.M. Speed, Prof Jesper Madsen, Dr Åshild Ø. Pedersen, Dr Ingunn M. Tombre & Prof René van der Wal (2016) Late snow melt moderates herbivore disturbance of the Arctic tundra, *Écoscience*, 23:1-2, 29-39, DOI: 10.1080/11956860.2016.1212684

To link to this article: <http://dx.doi.org/10.1080/11956860.2016.1212684>

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Late snow melt moderates herbivore disturbance of the Arctic tundra

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ABSTRACT

Resilience of tundra vegetation to disturbance by herbivores can be low and lead to ecosystem state shifts. Pink-footed geese *Anser brachyrhynchus* are the most numerous herbivore on Svalbard and disturb vegetation when foraging for below-ground plant biomass (grubbing). We assessed grubbing extent (occurrence of vegetation disturbance) and intensity (proportion of vegetation disturbed) in 2006/07/08 when goose numbers were approximately 56,000 and in 2013 when they increased to approximately 81,000. Despite a 36% increase in population size, in 2013 the grubbing extent at pre-breeding sites was similar to that in 2007/08 but grubbing intensity was lower. Extensive snow cover in 2013 probably dispersed geese over larger areas in search of snow-free patches for feeding, thereby reducing grubbing intensity. At the largest known breeding site, both grubbing extent and intensity increased with more geese. Birds preferentially fed close to nests in previously grubbed wet habitat, probably aiding nest defence and permitting feeding on plants that were easier to remove from the soil. A greater impact on tundra vegetation may occur at nesting areas if the breeding population continues to grow. However, timing of snowmelt appears key in moderating the impact of disturbance on tundra vegetation since it controls spatial distributions of feeding geese.

RÉSUMÉ

La résilience de la végétation de toundra à la perturbation par les herbivores peut être faible et mener l'écosystème à changer d'état. Les oies à bec court *Anser brachyrhynchus* sont les herbivores les plus nombreux du Svalbard et perturbent la végétation en fouillant le sol à la recherche de biomasse souterraine de plantes (déracinement). Nous avons déterminé l'étendue du déracinement (occurrence de végétation perturbée) et son intensité (proportion de végétation perturbée) en 2006, 2007 et 2008 quand le nombre d'oies était c. 56 000 et en 2013 quand il a augmenté à c. 81 000. Malgré une augmentation de 36% de la taille de la population, l'étendue du déracinement en 2013 aux sites avant accouplement était similaire à celle de 2007-2008, mais l'intensité du déracinement était plus faible. Le couvert nival extensif en 2013 a probablement mené les oies à se disperser sur une plus grande superficie à la recherche de parcelles à découvert pour s'alimenter, réduisant ainsi l'intensité du déracinement. Au plus grand site d'accouplement connu, l'étendue et l'intensité du déracinement ont augmenté avec le nombre d'oies. Les oiseaux s'alimentaient préférentiellement à proximité des nids dans les milieux humides précédemment déracinés, favorisant probablement la défense des nids et permettant l'alimentation sur des plantes plus faciles à retirer du sol. Un impact plus important sur la végétation de toundra pourrait survenir dans les aires de nidification si la population continue de croître. Toutefois, la période de fonte des neiges semble être un modérateur important de l'impact de la perturbation sur la végétation de toundra puisqu'elle contrôle la répartition spatiale des aires d'alimentation des oies.

ARTICLE HISTORY

Received 30 June 2016
Accepted 11 July 2016

KEYWORDS

Herbivory; vegetation shifts;
population increase;
environmental factors;
climatic change

MOTS-CLÉS


Herbivorie; changements de
végétation; augmentation
de population; variables
environnementales;
changement climatique

Introduction

A large increase in the population size of herbivores has the potential to cause extensive vegetation disturbance, triggering a shift in vegetation state from one

dominant type to another (Beisner et al. 2003; Van der Wal 2006), sometimes creating barren areas and ultimately a vegetation-free state (Van de Koppel et al. 1999; Myrsterud 2006). Apart from changes in

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 Supplemental data for for this article can be accessed at <http://dx.doi.org/10.1080/11956860.2016.1212684>

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population sizes, the other mechanism by which alternative stable states in vegetation may occur is via a change in a key environmental variable, such as rainfall, nutrient levels or temperature (Scheffer et al. 2001; Foley et al. 2003; Lenton 2013). Changes in herbivore population size and environmental conditions are not, however, mutually exclusive. Hence, they may either work in synchrony to produce alternative stable states, induced at tipping points different to that due to any one factor alone (Saccone et al. 2014), or may counteract one another, thereby stopping or slowing the transition from a vegetated state to a denuded and vegetation-free one.

In the Arctic, intensive grazing by sizeable numbers of both large and small herbivores has resulted in shifts in tundra vegetation states (Myrsterud 2006; Van der Wal 2006). An irruptive population of reindeer *Rangifer tarandus platyrhynchus* in Svalbard caused a marked vegetation shift from lichen to moss domination, with slow recovery of vascular plants and limited recolonisation of lichens (Hansen et al. 2007). A striking example of denudation due to combined changes in grazing pressure and environmental conditions has occurred in Canada, allowing increasing numbers of lesser snow geese *Chen caerulescens caerulescens* to cause extensive damage and destruction of saltmarsh vegetation. Such overgrazing by the geese increased water evaporation from the soil, leading to higher soil salinity, which inhibited plant growth (Jefferies & Rockwell 2002). The resultant habitat transitions which have occurred have had negative cascading effects on other species at the sub-arctic La Pérouse Bay breeding grounds (Jefferies & Rockwell 2002; Jefferies et al. 2004; Peterson et al. 2014). In the Arctic, one major environmental variable worth considering when assessing the potential for vegetation disturbance is spring snow cover. Greater snow cover, or late snowmelt, may protect some vegetation types but expose others to greater levels of herbivory (Stien et al. 2010; Anderson et al. 2012). In addition, snow cover extent and melt-out rate affect timing of breeding (Madsen et al. 2007), thereby influencing the use of and time spent at specific areas.

The Svalbard breeding population of pink-footed geese *Anser brachyrhynchus* has risen substantially since the 1970s due to improved winter survival as a result of conservation policies which have given the birds protection from hunting (Ebbinge et al. 1984). The population has continued to grow due to agricultural practices which have provided more food for the geese during the non-breeding season and, particularly over the last decade, a warmer climate on the breeding grounds (Kéry et al. 2006; Madsen et al. 2007; Jensen et al. 2014). Indeed, the

increase in population size means that pink-footed geese are now the most numerous migratory herbivore on Svalbard (see Madsen et al. 1999; Fox et al. 2010) and as such have the potential to cause substantial and extensive vegetation disturbance as a result of their feeding activities (Speed et al. 2009). The Svalbard-breeding population overwinters along the northern coastline of the Low Countries of Europe, migrating through Norway to arrive in Svalbard in mid-May (Fox et al. 2006). The arrival period to Svalbard is fixed to a one-week period in mid-May (Glahder et al. 2006), after which geese then spend a short time at pre-breeding staging sites (Fox et al. 2006; Glahder et al. 2006; Anderson, Hübner et al. 2015) before moving to their breeding grounds to initiate nesting when snowmelt allows access to their nest sites (Madsen et al. 2007). Early in the season, prior to the availability of sufficient above-ground plant material, geese feed by grubbing for the nutritious below-ground rhizomes and storage organs of Arctic tundra plants (Fox et al. 2006, 2007). In doing so, they create beak-sized holes in the moss-mat, causing disruption of tundra vegetation (Van der Wal et al. 2007; Speed et al. 2009). Where feeding activity is intense, such grubbing can leave large patches of tundra devoid of vegetation, exposing the soil substrate to the atmosphere and causing shifts in carbon storage and plant community composition (Sjögersten et al. 2008; Speed et al. 2010a, 2010b). Furthermore, pink-footed geese appear drawn to feed at the periphery of areas that have already been disturbed (Van der Wal et al. 2007), thereby increasing the size of vegetation-free areas. However, future trends in spring snow cover (including patterns of snow cover across the landscape and melt-out rates) may also be a key factor in controlling vegetation disturbance by pink-footed geese since prolonged snow cover occurs in wetter habitat, thereby prohibiting access to preferred forage areas (Anderson et al. 2012).

Here we report on an assessment of the impact and extent of pink-footed goose feeding activities on the tundra of central Svalbard during 2006–2008 and again in 2013, a period in which the population size of pink-footed geese increased by 36% (Madsen et al. 2013), and how any impacts may be modulated by the extent of spring snow cover. We evaluated the influence of foraging geese on vegetation via two measures: the intensity of foraging (proportion of an area of vegetation disturbed) and the extent of foraging (the presence or absence of grubbing across the landscape). Our study focused on three important spring pre-breeding staging sites and the largest known nesting area in Svalbard, thereby covering a number of key locations over a large area of central Svalbard. In addition to investigating changes in foraging intensity and extent, since pink-footed geese appear drawn to feed in areas

with previously disturbed vegetation (Van der Wal et al. 2007), we also assessed patterns of re-utilisation of feeding patches and the mechanisms behind this. We tested the following predictions: foraging intensity and extent at the pre-breeding staging sites and at the nesting area are greatest when the pink-footed goose population is greatest; at the breeding area, pink-footed geese are more likely to feed closer to the colony than further away; and plants in areas of previously disturbed vegetation are mechanically easier to remove from the soil substrate than those in undisturbed areas.

Methods

Study areas and goose population

Geese are the dominant herbivores of the Arctic (Van der Wal 2005), with the pink-footed goose being the most numerous on Svalbard (see Madsen et al. 1999; Fox et al. 2010). The population has increased rapidly in recent decades (Figure 1a; Madsen et al. 2013). In fact, the population almost doubled in the period between 2000 and 2012, reaching 81,500 individuals in the winter season of 2012/13 (Figure 1a; Madsen et al. 2013).

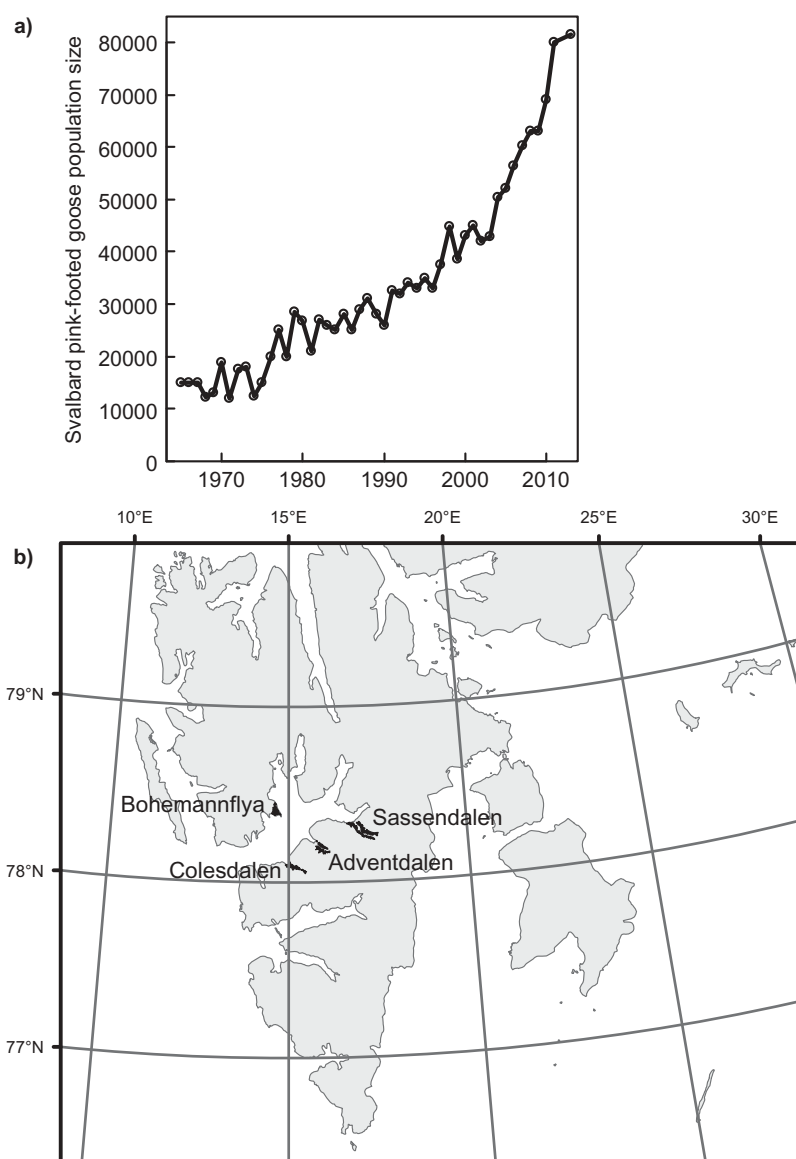


Figure 1. (a) Size of the Svalbard pink-footed goose population and (b) locations, in central Svalbard, of the four grubbing surveys (indicated in black).

Note: Population sizes were estimated during autumn/winter surveys in the overwintering area.

Source: Data from Madsen & Williams (2012) and Madsen et al. (2013).

Grubbing by pink-footed geese was surveyed in four different locations in central Svalbard: Adventdalen, Bohemannflya, Colesdalen and Sassendalen (Figure 1b). All sites are characterised by open tundra dominated by marsh, ridge and heath vegetation. Adventdalen, Bohemannflya and Colesdalen are used predominantly as pre-breeding staging sites by pink-footed geese when they first arrive in Svalbard in mid-May (Fox et al. 2006; Speed et al. 2009; Tombre et al. 2012), although a small number of geese do also breed in these areas. These sites are hereafter referred to as “pre-breeding sites”. Sassendalen is one of the main nesting areas for pink-footed geese in Svalbard (Jepsen et al. 2002) and is hereafter referred to as the “nesting area”.

Goose grubbing at pre-breeding sites

Pink-footed goose grubbing activity, carried out during early spring (mid-May–early June), was recorded at three pre-breeding sites (Colesdalen, Adventdalen and Bohemannflya; Figure 1b) in 2007 and 2013 (data for Adventdalen were also available from 2008). Eight transects (ranging in length from 1.1 to 1.9 km) were surveyed across the three pre-breeding sites. In total, 461 plots spaced at 30 m intervals along these transects were assessed in 2007, 213 in 2008 and 346 in 2013. Because of time limitations, the same transects were not re-surveyed each year; however, all later transects were located within the same boundaries of the original transects.

Grubbing was assessed using the same field method in all years. Along each transect, 5 m × 5 m plots, representative of typical patches of tundra habitat, were located at 30 m intervals. Grubbing was assessed within a 0.35 m × 0.35 m frame that was centrally located within each 5 m × 5 m plot because previous observations of feeding geese revealed that individual goose feeding stations were discrete and characteristically of such a smaller size. We evaluated two separate measures of grubbing along each transect: firstly, grubbing intensity, expressed as the proportion of the frame which was grubbed to the nearest 10%; and secondly, grubbing extent, assessed by recording the presence or absence of grubbing within each 0.35 m × 0.35 m frame. All measures of grubbing include only those from the spring of the current year in which transects were surveyed.

In our analyses we used vegetation types to define the landscape in terms of characteristics that are relevant to geese. We grouped *Dryas octopetala* ridge, *Cassiope tetragona* heath and *Luzula* spp. heath as dry habitat (over mostly free-draining and exposed soils);

graminoid sward (with *Poa* and *Festuca* spp.) and *Alopecurus borealis*/*Equisetum arvense* wet moss tundra as mesic habitat; and *Dupontia* spp./*Eriophorum scheuchzeri* marshes as wet habitat with very moist soils and patches of standing water.

To relate the two grubbing measures (extent and intensity) to the size of the pink-footed goose population, we used the population estimates from the autumn–winter prior to the spring grubbing season (Madsen et al. 2013). In order to correlate grubbing with the extent of spring snow cover across the landscape, we estimated for each location snow cover using MODIS satellite data (see later) for the years in which grubbing was assessed (2006, 2007, 2008 and 2013).

Goose grubbing at the nesting area

Pink-footed goose grubbing activity in different habitat types was also assessed in a key nesting area, Sassendalen, using the same estimates of grubbing intensity and grubbing extent as already described for pre-breeding sites. Two transects were surveyed in 2006 when the pink-footed goose population was 52,000 and snow cover was 49%. This was repeated in 2013 when the population was 81,500 and snow cover was 46% (Figure 1a). Transects ranged in length from 1.8 to 1.9 km, with 165 plots assessed in 2006 and 112 plots in 2013.

Since pink-footed geese effectively become central place foragers during the incubation period due to the need to defend nests against predators (Fox et al. 2007), we also determined the probability of grubbing in an area immediately adjacent to pink-footed goose nest sites. This allowed us to determine whether geese grubbed closer to their nests rather than further away and whether they grubbed in previously exploited tundra or moved to use undisturbed parts of the tundra. Eight transects, ranging in length from 10 m to 27 m, were assessed in Sassendalen in 2010, 2012 and 2013 (Figure 1b). Transects were located in wet fens, the preferred foraging habitat of pink-footed geese (Speed et al. 2009), and situated adjacent (10–250 m) to clusters of nests (range 3–30 nests per cluster). The initial selection of sites for grubbing analysis was determined by the presence of previous grubbing activity, fresh droppings and proximity to nests. The presence or absence of grubbing was recorded along the line of each transect at 1 cm intervals in 2010 and this was repeated in 2012 and 2013. All transects started at locations closest to nest sites and ran away from the colony.

Below-ground forage extractability

To determine how mechanically difficult it was for geese to remove the edible below-ground parts of typical forage plants (grasses *A. borealis* and *Dupontia* spp., and rush *E. scheuchzeri*), an artificial clamping mechanism was used to measure the force required to extract individual plants from the ground (see Anderson et al. 2012). Sampling was conducted during spring (mid-May–end of May). We selected previously grubbed vegetation by observing where groups of geese were feeding and had formed noticeably grubbed patches in the tundra vegetation. Vegetation which was of a similar composition to that which had been grubbed but was undisturbed was sampled to represent non-grubbed vegetation. Individual shoots of forage plants were selected for extraction, with those located at the outer edge of grubbed patches sampled for the previously grubbed vegetation category. Repeated sampling of the same areas and sampling of damaged shoots were avoided. The artificial clamping mechanism gripped an individual plant at the junction between the above-ground and below-ground parts and, when pulled directly vertically upwards, registered an extraction value in kilogrammes on a hanging balance. During sampling, some plants snapped at the junction of above-ground and below-ground parts, which then made it impossible to grip the remaining below-ground section of the plant and remove it from the soil substrate. Each sample was split into above-ground and below-ground components at the point at which live green tissue was observed. Samples were washed and oven dried at 70°C. Once stabilised, the weight was subsequently recorded. Below-ground biomass extraction values were calculated as the reading recorded from the hanging balance (in kilogrammes) divided by the dry weight (in grams) of the below-ground part of the plant removed from the soil in order to account for differences in sizes of below-ground plant parts and to make comparisons among species.

Spring snow cover analysis

Since snow cover affects where in the tundra geese can feed and prohibits access to preferred wetter habitats (Anderson et al. 2012), we assessed snow cover during late May in 2006, 2007, 2008 and 2013 through the use of cloud-free MODIS satellite images (spectral bands 1 [620–670 nm] and 2 [841–876 nm], resolution 250 m). It proved impossible to obtain cloud-free images for exactly the same date in each year, hence images used for analysis dated from a slightly wider period of time (23–26 May). No atmospheric correction was applied

and the MODIS Swath Reprojection Tool (LP DAAC 2016) was used to geo-reference each image. Since a previous study showed that the probability of grubbing in sampling plots located at elevations greater than approximately 250 m was zero (Pedersen et al. 2013), we restricted our snow cover estimates to elevations below this. Snow cover values for each image were estimated using visual training points and a maximum likelihood classification to generate a two-class (snow, no snow) standard confusion matrix, with no less than 50 points identified for each class. It is unlikely that every snow-free patch of vegetation was distinguishable in the MODIS images at a resolution of 250 m. However, the images enabled us to give an overall estimate of snow cover across each site and hence a good indication of how much of the landscape below an elevation of 250 m was available for goose foraging and how that availability differed among years. We did not find any correlation between the date of image capture (day of year) and snow cover estimate at any of the survey locations (Adventdalen: $r = 0.14$, $p = 0.86$; Bohemannflya: $r = 0.24$, $p = 0.76$; Colesdalen: $r = -0.16$, $p = 0.85$; Sassendalen: $r = 0.20$, $p = 0.80$). Hence, we have assumed that the prevailing low temperatures (at or below freezing) and minimal precipitation in days prior to and after image acquisition caused minimal error in our estimates of annual snow cover and that the images were representative of snow conditions at the same date from year to year and are therefore comparable.

Statistical methods

All statistical analyses were carried out in R version 3.1.1, using the mixed model packages *glmmADMB* (Skaug et al. 2014) for modelling grubbing intensity and *lme4* (Bates et al. 2014) for modelling grubbing extent across different habitat types at the pre-breeding staging sites and the nesting area. The generalised linear mixed models for both pre-breeding sites and the nesting area used a beta distribution and logit link function to determine grubbing intensity and a binomial distribution and logit link function to determine grubbing extent.

At the pre-breeding staging sites, both the grubbing intensity and the grubbing extent models used year (2006, 2007, 2008, 2013), staging site (Adventdalen, Bohemannflya, Colesdalen) and habitat type (dry, mesic, wet) as fixed effects and transect number as the random effect. This allowed us to determine whether grubbing intensity and grubbing extent differed between years, staging site and habitat type. At the nesting area, both grubbing intensity and grubbing extent models were

the same as the pre-breeding staging site models, with the exclusion of staging site as a fixed factor. This allowed us to determine whether grubbing intensity and grubbing extent differed between years and habitat type.

When determining the probability of grubbing immediately adjacent to nest sites we used generalised linear mixed models with binomial distribution and logit link function. We ran two models to determine: whether geese grubbed closer to their nests as opposed to areas further away; and whether birds grubbed in areas that had previously been used for grubbing or if they moved to use undisturbed areas. Fixed effects were distance along the transect from the nest in the first model and distance from the nearest grubbing patch in the second model, with transect number as the random effect in both models.

An analysis of variance was used to compare the mean extraction forces required to remove the below-ground biomass of forage plants growing in previously grubbed areas with those growing in undisturbed areas of the tundra within the same habitat type. We included species as a factor to determine whether there were any differences in extraction forces between forage species.

Results

Goose grubbing at pre-breeding sites

Grubbing intensity

Despite the considerable increase in the numbers of the pink-footed geese using Svalbard, grubbing intensity was significantly lower in 2013 than in 2007/08 at all pre-breeding staging sites ($t_{246} = -3.31$, $p = 0.001$; Figure 2a–c). However, the lower grubbing intensity in 2013 did coincide with a period of greater spring snow cover (Table 1). Thus, when spring snow cover increased by 17% at Adventdalen and Colesdalen, the probability of grubbing decreased by 4%, while at Bohemannflya it decreased by 7% when spring snow cover increased by 7%.

Grubbing extent

The extent of grubbing (as measured within the surveyed transects) at the pre-breeding sites was similar between study years ($t_{938} = 0.12$, $p = 0.90$; Figure 2e–g) despite snow cover differing. Geese displayed a preference for grubbing in wetter parts of the tundra at all

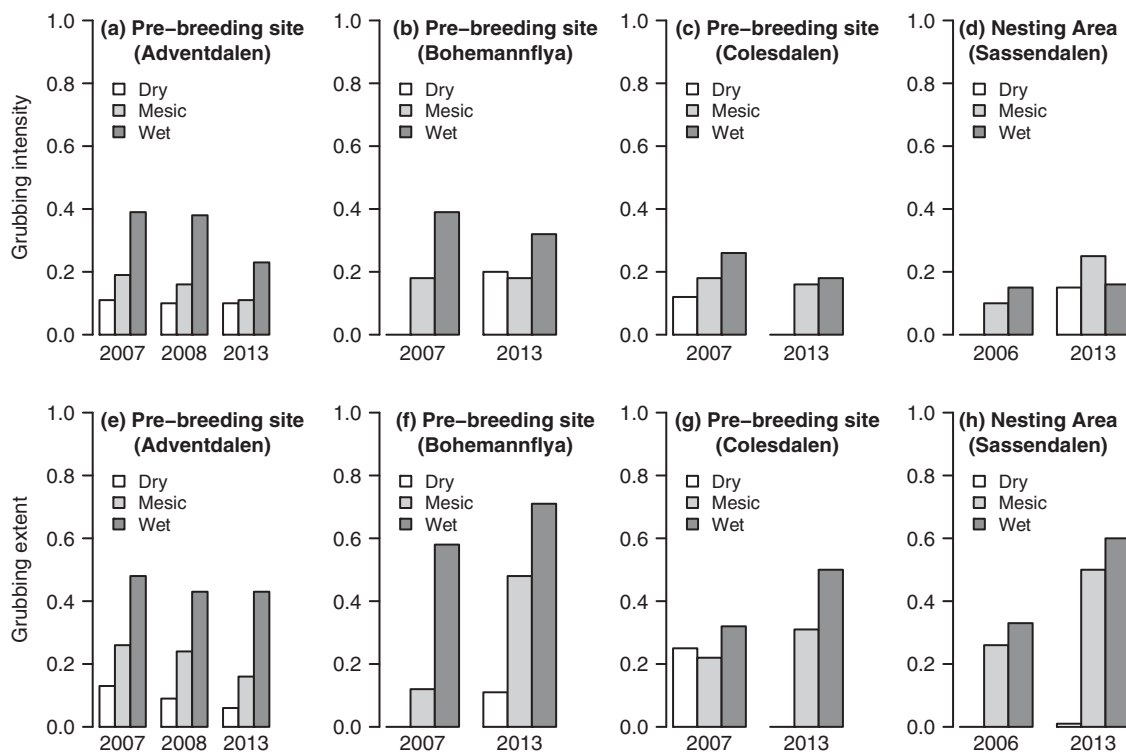


Figure 2. Grubbing intensity and extent at pink-footed goose pre-breeding sites and nesting site in Svalbard in 2006, 2007, 2008 and 2013. Top row shows grubbing intensity at three pre-breeding sites: (a) Adventdalen, (b) Bohemannflya and (c) Colesdalen in 2007, 2008 (Adventdalen only) and 2013; and at the nesting area (d) Sassendalen in 2006 and 2013. Bottom row shows grubbing extent at the same three pre-breeding sites: (e) Adventdalen, (f) Bohemannflya and (g) Colesdalen in 2007, 2008 (only Adventdalen) and 2013; and at the nesting area (h) Sassendalen in 2006 and 2013.

Note: White bars indicate dry habitat, light grey bars indicate mesic habitat and dark grey bars indicate wet habitat.

Table 1. Derived snow cover estimates (%) obtained from MODIS satellite images taken of the three pre-breeding sites (Adventdalen, Bohemannflya, Colesdalen) and at the nesting site (Sassendalen) for each of the years when grubbing was assessed (2006–2008, 2013).

Year	Pre-breeding sites			Nesting site
	Adventdalen	Bohemannflya	Colesdalen	Sassendalen
2006	–	–	–	51
2007	35	39	33	–
2008	48	–	–	–
2013	52	46	50	46

Note: It was impossible to obtain cloud-free images for exactly the same date in each year, hence images used for analysis dated from 23 to 26 May. Snow cover estimates were restricted to elevations below 250 m since the probability of grubbing in sampling plots located at elevations greater than this was zero (Pedersen et al. 2013). Snow cover values for each image were estimated using visual training points and a maximum likelihood classification to generate a two-class (snow, no snow) standard confusion matrix, with no less than 50 points identified for each class. We generated masks to delineate the areas of interest to ensure the same geographic area was assessed in different years.

three pre-breeding sites and regardless of the amount of spring snow cover ($F_{2,254} = 3.15$, $p = 0.05$), with 52% of wet habitat grubbed, compared with 24% of mesic and 10% of dry along the transects.

Goose grubbing at the nesting area

Grubbing intensity

At the nesting area, grubbing intensity was greater in dry and mesic habitats during the more recent survey ($z = 2.57$, $p = 0.01$; Figure 2d), but remained similar in wet habitat (Figure 2d), probably as a result of restricted access to wet areas due to more extensive snow cover in 2013 than in 2006.

Grubbing extent

Over the same period the extent of grubbing at the nesting area almost doubled in mesic (from 26 to 50%) and wet habitats (from 33 to 60%; $t_{230} = 3.82$, $p < 0.001$; Figure 2h) but remained negligible in dry areas (from 0 to 0.01%; Figure 2h). These changes occurred simultaneously with a 57% increase in the pink-footed goose population (Figure 1a).

Grubbing location in relation to nest sites

Close to nest sites, approximately 30–40% of patches grubbed in 2010 were used again in 2012 and 2013, although patches over 2 m away from the nearest grubbed tundra in 2010 were almost never used for grubbing in the latter years. Hence, geese were significantly more likely to grub close to existing grubbed patches or within areas which had previously been used for grubbing, compared with undisturbed ground (2012: $z = -31.7$, $p < 0.001$; 2013: $z = -24.1$, $p < 0.001$; Figure 3a,b): 23–35% of wet fens immediately adjacent to nests were grubbed, whilst this was only 5–12% for wet fens at the maximum distance of 27 m away from nests sites. The probability of grubbing decreased significantly with increasing distance from nest sites (2010: $z = -14.6$, p

< 0.001 ; 2012: $z = -19.1$, $p < 0.001$; 2013: $z = -8.74$, $p < 0.001$; Figure 3c).

Below-ground forage extractability

The force needed to extract below-ground plant material was significantly reduced for locations that were previously grubbed ($F_{3,64} = 25.2$, $p < 0.001$). This was clearest for *Dupontia* spp. and *E. scheuchzeri*, which were 30–50% easier to remove from the soil substrate in previously grubbed tundra than in undisturbed tundra ($t_{26} = 3.52$, $p = 0.02$; $t_{22} = 2.84$, $p = 0.04$, respectively; Figure 4). For *A. borealis* there appeared to be no significant difference in the extraction forces required to remove this species from grubbed and undisturbed tundra ($t_{16} = 1.87$, $p = 0.12$; Figure 4), although this may be due to relatively low sample size for this species. When considering plant extraction solely within a grubbed system, the same force was required to remove all species tested (*A. borealis*: 39.2 kg per g; *Dupontia* spp.: 30.5 kg per g; *E. scheuchzeri*: 45.0 kg per g; $F_{2,64} = 0.62$, $p = 0.56$; Figure 4).

Discussion

One of the most striking outcomes of an increase in abundance of an Arctic herbivore has been the dramatic shift in vegetation state witnessed across areas of the tundra used by large numbers of lesser snow geese (Jefferies & Rockwell 2002). This event now acts as a warning for other parts of the Arctic tundra that experience marked population increases of herbivores (Jefferies et al. 2003). In light of the findings from the lesser snow geese system, it is perhaps somewhat surprising that our expectations of more vegetation disturbance, particularly in the preferred wetter parts of the Svalbard tundra (Anderson et al. 2012), due to larger numbers of pink-footed geese was not universally observed. In fact, it appears that over the time in which the population size has risen, a clear increase in grubbing has only been

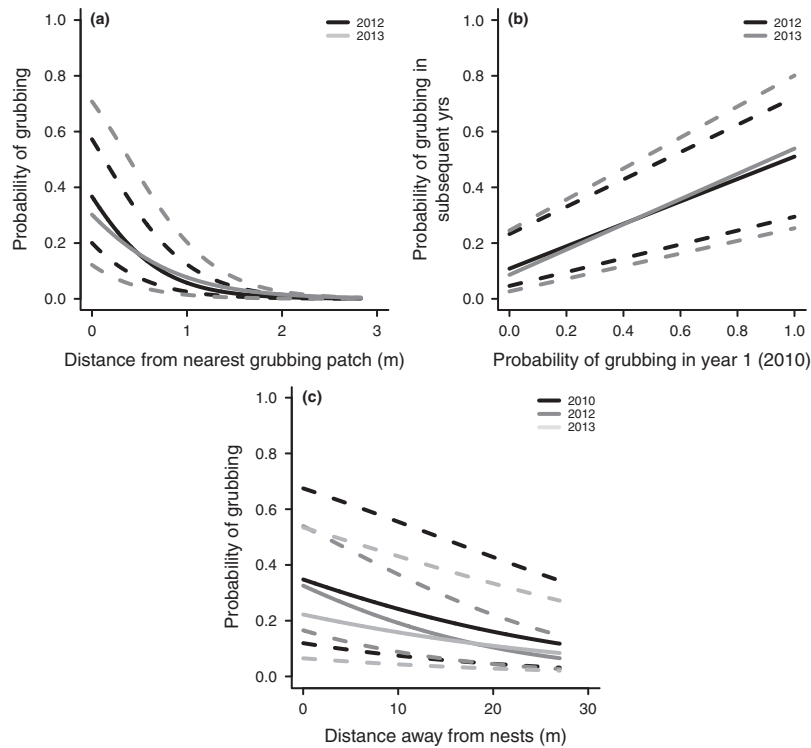


Figure 3. Probability of pink-footed goose grubbing at the nesting area in wet fen habitat in Sassendalen, Svalbard. (a) Probability of grubbing in 2012 and 2013 related to the distance (m) from nearest grubbing patches measured in the reference year 2010. (b) Probability of grubbing in 2012 and 2013 related to the probability of grubbing in the reference year 2010. (c) Probability of grubbing in 2010, 2012 and 2013 related to distances from nest sites.

Note: Dashed lines indicated 95% confidence limits.

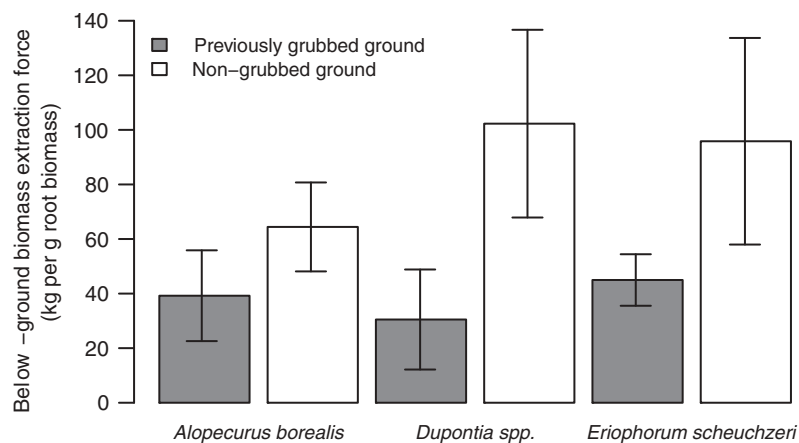


Figure 4. Below-ground biomass extraction forces per equivalent mass of root biomass for three pink-footed goose forage species.

Note: Bars indicate 95% confidence limits.

Source: Data for samples from “non-grubbed ground” from Anderson et al. (2012).

observed at the nesting area, where birds may be constrained to more short-range usage of the tundra near their nest site. It seems that spring snow cover extent, a factor known to influence goose foraging (Anderson et al. 2012), is a key moderating factor for grubbing activity, and thus is far more influential in relation to vegetation disturbance of the tundra than goose population size.

A larger population size of Svalbard pink-footed geese means more birds were present and presumably feeding during spring at pre-breeding sites. Our findings indicate that the presence of a greater number of individuals did not lead to more birds concentrating their feeding in a given place. Rather, since snow cover and frozen substrate physically prevent access to

below-ground plant parts and prohibit grubbing (Fox et al. 2006; Anderson et al. 2012), or at the very least limit it to the shallow uppermost thawed layer, birds must have spread out across the landscape in search of areas that had already experienced some thawing of the soil substrate. Given that snowmelt is prolonged in wetter areas (Anderson et al. 2012), resulting in relatively little wet habitat being snow free compared with drier parts of the tundra, the preference geese displayed for feeding in wetter areas was rather unexpected based on habitat availability due to snow cover. However, this does give a better indication of the dynamic use of the tundra by feeding geese at the landscape scale: higher snow cover leads to geese being more dispersed across the landscape as they seek out snow-free wet habitat, thereby utilising more places, but less intensively, for feeding. Snow pack models, satellite-derived snow cover data and snow cover simulations indicate that in Arctic areas with a maritime climate, snow cover duration is likely to decrease throughout the twenty-first century (Brown & Mote 2009). Since Svalbard experiences a warmer climate than other areas at similar latitudes, due to the relatively warm waters that reach the west coast of the archipelago (Rønning 1996), an ongoing reduction in snow cover duration can be expected (Brown & Mote 2009). Hence, the important moderating effect of snow cover on vegetation disturbance by pink-footed geese may lessen in coming years.

In contrast to pre-breeding sites, over a large spatial scale at the nesting area both grubbing intensity and grubbing extent were higher in 2013 than in 2006. During this time, the population increased by more than 30%, and nest numbers within the goose colony at this site more than doubled from 94 to 210 (Anderson, Madsen et al. 2015). The role of snow cover here is difficult to assess because we were only able to compare 2013 with 2006, a year in which snow conditions were similar and observational data on goose foraging behaviour from the breeding period are limited. Foraging activities immediately prior to the breeding period remains a topic in need of more research in order to unpick the combined effects of snow cover and population size on vegetation disturbance by pink-footed geese at their nesting areas. At the smaller spatial scale, we found that the probability of grubbing declined with increased distance from the nest. During the nesting period that lasts 26–27 days adult birds only take short recess periods to feed when necessary, although the male will take the opportunity to feed nearby while guarding the incubating female (Løvenskiold 1964; Inglis 1977). This is probably because incubating birds are constrained in their use

of the tundra to the vicinity of their nests as feeding in such places allows adults to promptly return to the nest if approaching predators are observed. Hence, such behaviour aids in nest defence, leading to significantly higher nesting success rates compared with geese nesting in those locations where forage areas are far away from the nest (Anderson, Madsen et al. 2015). Additionally, in results which substantiate the findings of Esselink et al. (1997) and Van der Wal et al. (2007), we found that previously grubbed wet tundra was more likely to be re-grubbed than undisturbed wet tundra. Our findings, however, move a step further in revealing the mechanism for re-grubbing: it is mechanically easier to remove below-ground biomass of key forage plants from the soil substrate in previously grubbed wet areas than in “pristine” undisturbed wet tundra. It is important to highlight that, rather than the tundra as a whole, it is wet habitat in Svalbard which may be at an increased risk of disturbance and state or community compositional change due to the grubbing activities of pink-footed geese.

The de-vegetation of parts of the Canadian Arctic by lesser snow geese (Jefferies & Rockwell 2002) has raised the possibility of a similar situation occurring with pink-footed geese in Svalbard (Madsen & Williams 2012; Pedersen et al. 2013). Within the International Species Management Plan implemented under the auspices of the African–Eurasian Waterbird Agreement (Madsen & Williams 2012), a population target of 60,000 pink-footed geese has been agreed between the range states. This agreement was made to avoid conflicts with agricultural interests in the staging and wintering areas, as well as reducing any possible degradation of Svalbard tundra vegetation. As a first, large-scale assessment of trends in vegetation disturbance caused by grubbing in Svalbard, this study suggests that the extent of spring snow cover moderates the intensity of grubbing by pink-footed geese at pre-breeding sites. However, it seems that increasing numbers of pink-footed geese may have some impact on wet habitat vegetation at the nesting area, probably due to an increase in the number of birds using the colony and constraint in the use of the tundra to areas closer to their nests. Nevertheless, although the extent of grubbing in wet habitats at both pre-breeding sites (with signs of grubbing observed in 43–71% of all sampling plots) and the nesting area (up to 60%) appears high, grubbing intensity remains relatively low. This suggests that the true spatial extent of grubbing across the Svalbard landscape may be patchy and localised with, as yet, no wide-scale damage to the tundra from goose feeding activities. Hence, as intimated by Jefferies and Drent (2006), it appears that, in Svalbard at least, we are not dealing with a scenario similar to that found with lesser snow

geese in the Canadian Arctic. Pink-footed geese respond to differing snow cover conditions through flexible use of the landscape; for example, by initiating nesting earlier when snow cover is low (Madsen et al. 2007) or by remaining at pre-breeding sites when snow cover is high (Anderson, Hübner et al. 2015). Therefore, future changes in spring snow conditions (extent of cover and melt-out rates) is likely to have a strong influence on where grubbing and its impacts on vegetation are felt most at the landscape scale (i.e. whether at pre-breeding sites or at nesting areas), particularly since the timing of the spring migration is unaffected by temperature conditions in continental Europe during early spring (see Supplementary material). To determine whether the Svalbard tundra remains relatively resilient to vegetation damage from feeding pink-footed geese, continued monitoring of environmental conditions and habitat disturbance due to grubbing activities at both pre-breeding and nesting sites as well as goose densities and population sizes are required, particularly since the tipping points for changes in vegetation states in this system are as yet unknown.

Acknowledgements

The authors thank the Governor of Svalbard for granting access to study areas and Troels Hastrup, Juliet Blum and Malcolm Parsons for field assistance. Two anonymous reviewers are thanked for constructive comments on the manuscript.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This project was supported by the Svalbard Environmental Protection Fund [project number 12/118] and the Fram Centre (the Climate ecological Observatory for Arctic Tundra project in the Terrestrial Flagship).

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